Research Note

No. 94 1984

ISSN 0226-9368

Effects of snowshoe hare damage on juvenile lodgepole pine - Implications for spacing natural stands

by
Thomas P. Sullivan

Province of British Columbia
Ministry of Forests

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Canadian Cataloguing in Publication Data

Sullivan, Thomas Priestlay, 1951-
Effects of snowshoe hare damage on juvenile lodgepole pine

(Research note, ISSN 0226-9368 ; no. 94)

Bibliography: p.
ISBN 0-7718-8441-9

1. Lodge-pole pine - Wounds and injuries. 2. Forest thinning. 3. Wildlife depredation - British Columbia - Prince George Region. 4. Lepus americanus. I. British Columbia. Ministry of Forests. II. Title. III. Series: Research note (British Columbia. Ministry of Forests) ; no. 94.

634.9'751669322'097112
SB608.L6S94 1984 C84-092201-9

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Published by the

Information Services Branch
Ministry of Forests
Parliament Buildings
Victoria, B.C.
V8W 3E7

Copies of this and other Ministry of Forests titles may be purchased from Queen's Printer Publications, Parliament Buildings, Victoria, B.C., V8V 4R6

ABSTRACT

This study measured the impact of snowshoe hare (Lepus americanus Erxleben) feeding on lodgepole pine (Pinus contorta Dougl. var. latifolia Engelm.) during the first four years after spacing. An 18-year-old stand, 20 km east of Prince George, B.C., was manually spaced (2 m x 2 m) in 1979. Hare feeding damage and populations were monitored from 1979 to 1983 in the spaced and a nearby control (unspaced) stand. The study period corresponded with the late increase, peak, and decline phases of the 10-year hare population cycle. Negligible damage to crop trees was recorded in the first winter after spacing, as hares fed on the foliage from felled trees. Feeding attacks on spaced trees increased dramatically (74.8% trees damaged) in the subsequent winter before declining to 18.5% and 14.3% during the third and fourth winters, respectively. Damage to unspaced crop trees varied from 24.5% to 69.1% during this period.

The total percentage of girdled and semi-girdled ($\geq$ 50% of circumference) stems was 18.1% in the spaced and 30.1% in the control stand. Semi-girdling (sub-lethal) damage clearly suppressed diameter growth of crop trees in both stands. The total amount of bark and vascular tissue removed did not appear to affect diameter growth during the first three years after spacing. The spatial distribution of girdling and semi-girdling injuries tended to be clumped over the area of the control stand. In general, the frequency of attack and proportion of girdled and semi-girdled trees were significantly greater among small (< 60 mm dbh) than large trees. Trees larger than 60-80 mm diameter received little feeding damage from snowshoe hares. Stands with fewer than 15 000 stems/ha have relatively large average diameters, and hence may be spaced with little compensation for future crop tree loss to hares. Several silvicultural recommendations are suggested to alleviate hare damage to spaced lodgepole pine.

Key Words: lodgepole pine, juvenile spacing, snowshoe hare, intensive silviculture, barking, girdling, feeding damage, 10-year population cycle, British Columbia.

ACKNOWLEDGEMENTS

I thank D.S. Sullivan, W. Kaiser, R. Moses, J. Krebs, and C. Robinson for field assistance. L. Herring and H. Coates of the Ministry of Forests, Prince George, provided logistical support and conducted the damage assessments.

TABLE OF CONTENTS

Abstract iii

Acknowledgements iv

Introduction 1

Methods 2
- Stand Selection and Site Description 2
- Sampling Design and Tree Measurement 3
- Lodgepole Pine Damage Assessment 5
- Snowshoe Hare Populations 6
- Statistical Analysis 6

Results and Discussion 10
- Lodgepole Pine Damage 10
- Impact of Bark and Vascular Tissue Removal on Growth and Survival 11
- Distribution of Damage 17
- Snowshoe Hare Populations 18
- Snow Depth 21

Conclusions 21

Recommendations to Alleviate Damage 23

Literature Cited 25

TABLES

1. Summary of statistical analyses as reported in text 7

2. Percentage of trees damaged by snowshoe hares during the winter of 1979-80 in a mixed fir-pine stand 12

FIGURES

1. Crop tree diameter and height classes of lodgepole pine in control and spaced stands, Bowe Creek, 1979 4

2. Percentage of crop trees damaged by snowshoe hares during five overwinter periods, in control and spaced stands 9

3. Percentage of girdled, semi-girdled, and undamaged crop trees in control and spaced stands of lodgepole pine, 1979-83 .. 13

4. Relationship between percent circumference girdled and stem diameter, impact of semi-girdling on loss of diameter increment, and 3-year diameter increments in control and spaced stands 14

FIGURES cont'd.

5. Total amount and average amount per tree of bark and vascular tissues removed by hares during five overwinter periods, in control and spaced stands 15

6. Population densities (MNA) of snowshoe hares in control and spaced stands 19

7. Relationship of new snowshoe hare damage intensity, phase of population cycle, and snow depth, for control and spaced stands during 1979-83 20

INTRODUCTION

Juvenile spacing will concentrate growth on a predetermined number of stems that have been selected for superior growth and form. This spacing places future crop trees in possession of a site at an early age of stand development, by eliminating their less desirable competitors. Numerous natural stands of young lodgepole pine (Pinus contorta Dougl. var. latifolia Engelm.) located in the central interior of British Columbia are suitable for juvenile spacing.

Many stands of lodgepole pine covering the Grove Burn (which occurred in 1961) in the Prince George Forest Region have been spaced as part of the Intensive Forest Management Program. There is severe animal feeding damage in many of the untreated stands in this area. Animal damage has also been observed in similar stands of lodgepole pine in the Cariboo and Prince Rupert Forest Regions.

The most serious damage at Prince George may be categorized as barking injuries to the basal and sometimes upper sections of trees. The snowshoe hare (Lepus americanus Erxleben) has caused the majority of basal barking injuries in stands. Of secondary importance, at this time, is the red squirrel (Tamiasciurus hudsonicus Erxleben) which has caused some damage to the basal and upper parts of trees. Snowshoe hare barking and girdling injuries to coniferous stems have been recorded by several authors (Bider 1961; Lawrence et al. 1961; de Vos 1964; Lloyd-Smith and Piene 1981). A detailed description of hare and squirrel barking injuries to lodgepole pine in central B.C. has been discussed by Sullivan and Sullivan (1982a); and, in Alberta reported by Johnstone (1981a) and Powell (1982). In general, overstocked pine stands provide optimum habitat for snowshoe hares (Adams 1959; Grange 1965; Koehler et al. 1979). These hares reach a peak in abundance every 9-10 years and may cause a serious damage problem for crop trees in natural and thinned stands of lodgepole pine. Sullivan and Sullivan (1983) provided an index of pine density levels which may be susceptible to hare damage when stands are operationally spaced.

Successful spacing programs must leave an optimum number of trees per given area to ensure maximum wood production. Therefore, spacing must take into account subsequent mortality factors. Hare damage could substantially reduce the number of stems per unit area below the optimum level. If this animal damage is not taken into account, then spacing may not produce the desired increased growth and yield.

This study was designed to determine the extent of snowshoe hare damage in treated (spaced) and untreated (control) stands of lodgepole pine near Prince George, B.C. The major objective was to determine how much damage individual trees can sustain before growth is seriously hindered or they are killed. In addition, population densities of hares were monitored in control and treatment stands. This information is of importance with respect to the 10-year cyclic fluctuation in abundance of hares, and how this relates to extent of damage to crop trees in spaced stands.

METHODS

Stand Selection and Site Description

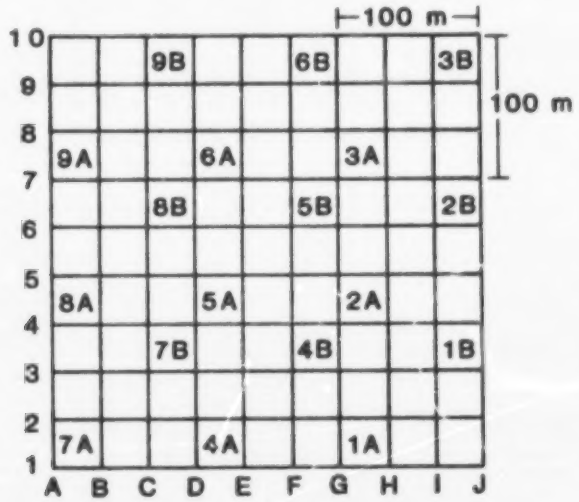
This study was located at Bowes Creek on the Grove Burn (of 1961), 20 km southeast of Prince George in the Sub-boreal Spruce Biogeoclimatic Zone (Krajina 1969). This area (32 400 ha) was covered by a mixture of young lodgepole pine stands and several deciduous species: willow (Salix L. spp.), aspen (Populus tremuloides Michx.), black cottonwood (P. trichocarpa [Torr and Gray ex Hook] Brayshaw), paper birch (Betula papyrifera Marsh.), and Sitka alder (Alnus sinuata (Regel) Rydb.). The site is sandy loam gleyed gray luvisol on a level valley floor at 760 m.

The average density of lodgepole pine in the control stand in 1979 was 34 778 stems/ha (range: 4000 to 140 000; n=18). The average density of lodgepole pine in the treatment stand prior to spacing was 40 000 stems/ha (range: 2000 to 100 000; n=27), and after spacing was 2304 stems/ha. The number of crop trees, by height and diameter classes, for the control and

treatment stands (prior to spacing) is illustrated in Figure 1. In general, there were signficantly more large-diameter crop trees (but fewer small-diameter ones) in the control (average 56.5 mm), than in the treatment (average 49.9 mm). Similarly, the mean height of the control stand (564.8 cm) was significantly taller than that of the treated stand (540.4 cm).

Sampling Design and Tree Measurement

Two 9-ha matrix grids (one control and one treatment) were established during March 1979 in natural stands of lodgepole pine at Bowes Creek. Each grid had 18 permanent tree sampling plots located as follows:



Two circular sampling plots (50 m^2) were systematically located within each of the 1-ha segments of each grid area. The size of these plots allowed for sampling of up to 15 crop trees per plot. All potential crop trees in the 50 m^2 plots on control and treatment grids were permanently tagged. Crop trees in the control area were chosen on the basis that these trees would be left as the future crop if the stand was spaced. Measurements of the height, diameter, and damage for all trees were done at the initial sampling period, 29 May - 28 June, 1979. Height and diameter measurements were taken again in

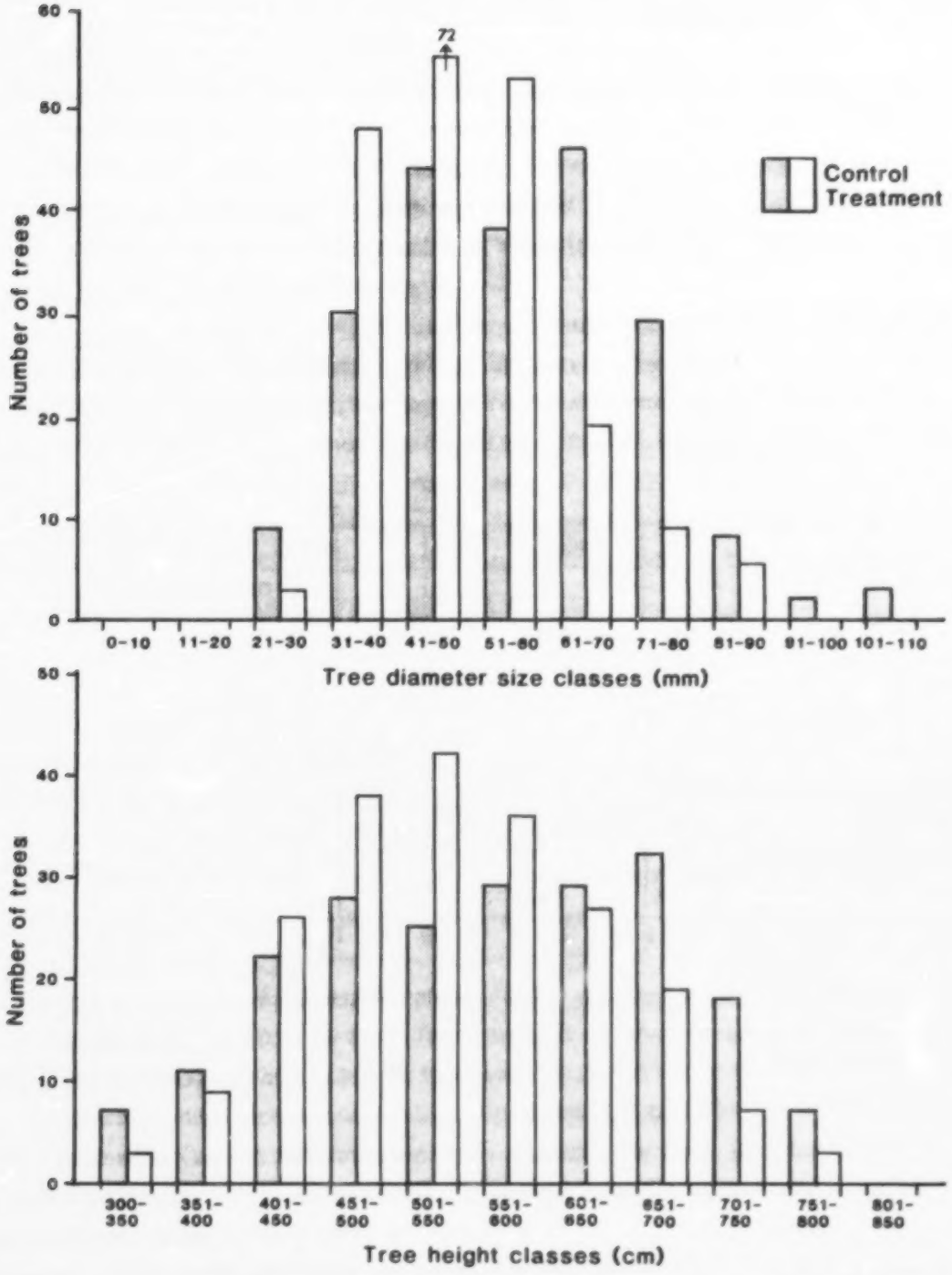


FIGURE 1. Crop tree diameter and height classes of lodgepole pine in control and spaced stands, Bowes Creek, 1979.

October 1982, a 3-year interval after this initial sampling time. The 50 m^2 plots on the treatment grid were manually spaced (2 m x 2 m) on 7-9 August, 1979. The entire treatment area (11.7 ha) was manually spaced (2 m x 2 m) during the period 27 August to 26 September, 1979.

Lodgepole Pine Damage Assessment

Assessments of snowshoe hare damage (barking, girdling) to lodgepole pine crop trees were done in the spring of each year. The maximum height (measured in centimetres) and width (circumference measured in millimetres) of each damage wound were recorded. The location of the center of each wound was recorded with respect to diameter of a given tree and marked with an individually coloured thumbtack. This allowed each wound to be identified and remeasured (if necessary) at subsequent sampling times. All new wounds were marked and recorded at each sampling time.

Each wound was identified with respect to the animal responsible (hare, squirrel, or "unknown") and to whether the damage was old (prior to fall of 1978) or new (since the fall of 1978). All unknown damage was classed as old when tree resins had covered the wound and obscured the damage characteristics.

The width of each wound, as a percentage of the circumference of a stem at that point, was used to assess girdling injuries to crop trees. The maximum percentage of circumference girdled was calculated for each tree and divided into the following classes: 0-49, 50-75, 76-99, and 100%. Trees having wounds with a damaged circumference $\geq$50% (semi-girdled) were considered likely to have reduced growth and yield, or even to die at some time in the near future. Trees that were completely girdled would, of course, die. The area of each wound, and hence area of bark and vascular tissues removed per given tree, was also calculated to assess both the effect on growth and yield, and the tree's susceptibility to fungal attack. Diameter increment, rather than height growth, was used to assess the impact of damage because of its more consistent response in lodgepole pine spacing experiments (Johnstone 1981a, 1981b, 1982).

Snowshoe Hare Populations

Populations of snowshoe hares were monitored at approximately 4-week intervals in summer and 8-week intervals in winter on the control and treatment grids. Each grid had 100 trap stations (10 x 10) with one live-trap (23 x 23 x 80 cm) at every other station. Extra traps were supplied as required to census high-density populations in 1979 and 1980. Grids were trapped for two nights during each sampling period. Traps were set on day 1, checked on days 2 and 3, and then locked open between trapping periods. All animals captured were ear-tagged with individually numbered metal tags and the point of capture was recorded.

The best estimate of population size from mark and recapture sampling is minimum number of animals known to be alive (MNA) at each trapping period. If x number of animals captured at time t are not caught at $t + 1$, but are recaptured at $t + 2$, then these x animals are alive but not censused at $t + 1$ and so should be included in the density estimate for that time. Enumeration techniques provide sufficiently accurate estimates for a trapping design in which 80% or more of the animals are caught at each sampling time (Hilborn *et al.* 1976). Trappability was considered to be high enough in this study to use minimum number alive estimates.

Statistical Analysis

A summary of all statistical analyses is presented in Table 1. Categories are outlined for the analysis of control versus treatment parameters, as well as for the comparison of annual measurements. Percentage data were transformed by arcsin square root prior to analysis. In all analyses, the level of significance is at least $p < 0.05$.

Analysis of variance was used to detect significant differences between control and treatment stands for mean diameter, mean height, 3-year diameter increments, and spatial distribution of damage. Comparisons of mean values were made using Duncan's new multiple range test. Analyses of the effect on diameter increment of semi-girdling and girdling, as well as of the amount of

TABLE 1. Summary of statistical analyses as reported in text

Levels of significance: *$p < 0.05$; **$p < 0.01$; NS $p > 0.05$.

Comparison or parameter	Test	% or $\bar{x} \pm$ Se or r (Sample size in parentheses)		Significance: control vs. spaced
		Control	Spaced	
Tree diameter (mm)	ANOVA	56.5 ± 1.2 (208)	49.9 ± 0.8 (210)	**
Tree height (cm)	ANOVA	564.8 ± 7.8 (208)	540.4 ± 6.6 (210)	*
Proportion crop trees damaged (Figure 2)	Chi-square	1979: 34.9 (208)	32.9 (210)	NS
		1980: 57.4 (204)	2.9 (210)	**
		1981: 69.1 (194)	74.8 (210)	NS
		1982: 54.3 (184)	18.5 (189)	**
		1983: 24.5 (184)	14.3 (189)	*
		** * ** **	** ** **	
Proportion crop trees damaged vs. diameter (Figure 2)	Linear regression	1979: -0.93**	-0.80*	
		1980: -0.96**		
		1981: -0.79*	-0.96**	
		1982: -0.94**		
		1983: -0.93**		
Proportion girdled vs. diameter (Figure 3)	Linear regression	-0.93** (208)	-0.94** (210)	

TABLE 1. Cont'd.

Comparison or parameter	Test	% or $\bar{x} \pm$ Se or r (Sample size in parentheses)		Significance: control vs. spaced
		Control	Spaced	
% circumference girdled vs. diameter (Figure 4A)	Linear regression	-0.58** (208)	-0.36** (210)	
Effect of semi-girdling injuries on diameter increment (mm) (undamaged vs. damaged crop trees) (Figure 4B)	t-test	13.6 ± 0.7 (18)	10.9 ± 0.9 (17)	**
		14.8 ± 1.7 (8)	10.0 ± 2.0 (8)	*
		15.9 ± 0.9 (32)	13.8 ± 3.9 (6)	NS
Diameter increment (mm) (Control vs. spaced) (Figure 4C)	ANOVA	13.6 ± 0.5 (177)	15.2 ± 0.4 (183)	**
Effect of bark and tissue removal on diameter increment (mm) (undamaged vs. damaged crop trees)	t-test	14.2 ± 0.7 (22)	15.4 ± 0.7 (50)	NS
		15.9 ± 1.0 (30)	18.9 ± 1.2 (34)	*
Tree diameters among plots	ANOVA	-	-	**
Semi-girdling damage among plots	ANOVA	-	-	**
Distribution of semi-girdling damage	Coefficient of dispersion	1.64	1.05	
Amount of bark and tissue removed among plots	ANOVA	-	-	NS

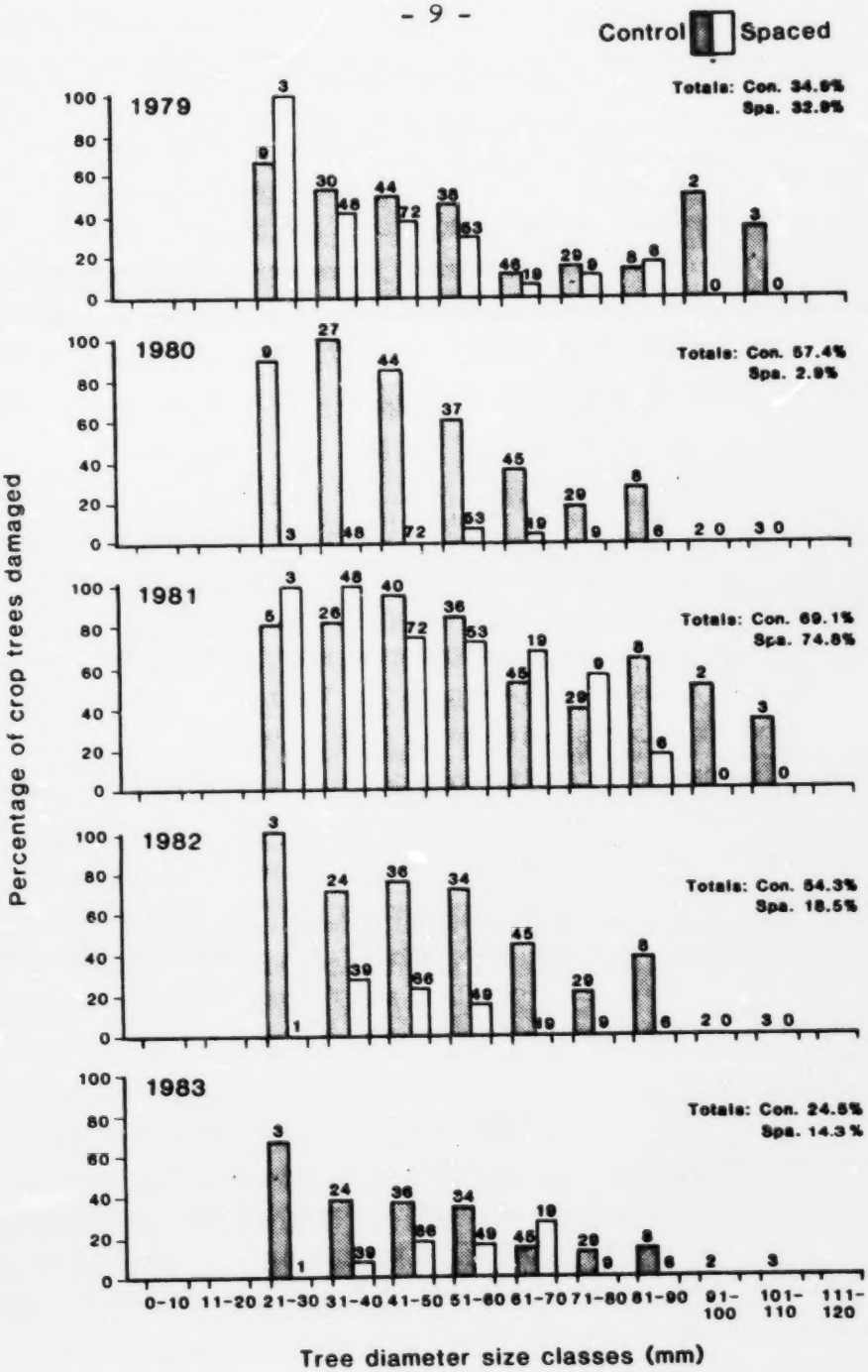


FIGURE 2. Percentage of crop trees damaged by snowshoe hares during five overwinter periods, in control and spaced stands. Sample size above each bar.

bark removed, used a t test for unpaired samples. Linear regression analysis was used to determine the effect of tree diameter on frequency of attack, proportion of girdled and semi-girdled stems, and percent circumference girdled. Chi-square tests were conducted to detect significant differences in the proportion of crop trees attacked in control and spaced stands as well as on an annual basis within each stand. A coefficient of dispersion (Sokal and Rohlf 1969) was used to assess the spatial distribution of damage within each stand.

RESULTS AND DISCUSSION

Lodgepole Pine Damage

The percentage of crop trees damaged each year by hares in control and treatment stands is illustrated in Figure 2. The total incidence of damage in the control stand increased significantly from 34.9% (1979) to 57.4% (1980) to 69.1% (1981). The damage intensity then declined significantly to 54.3% in 1982 and 24.5% in 1983. A similar progression would probably have occurred in the treatment stand but for the advent of spacing in 1979. Although a comparable level of damage (32.9%) occurred in the treatment stand prior to spacing, hares attacked very few crop trees (2.9%) during the subsequent winter of 1979-80. The felled pine slash and foliage from the spacing operation acted as an alternative food source, thereby preventing damage to the standing crop trees. Feeding attacks to spaced crop trees increased dramatically (74.8%) during the winter of 1980-81 because the alternative food source dried out during the previous summer. A similar result occurred in another (independent study) stand at Bowes Creek which was spaced in the fall of 1978. In the first winter (1978-79) after spacing, no feeding injuries resulted. However, the damage assessment in the spring of 1980 indicated that 38% of the pine and 14% of the fir crop trees were girdled (Table 2).

The intensity of damage in the spaced stand declined to 18.5% in 1981-82. This decrease was related to the declining hare population and the deep snow

(with its consequent lack of cover for hares) in the spaced stand. The percentage of crop trees damaged declined further to 14.3% in 1982-83. In all years in the control and when applicable (1979 and 1981) in the treatment stand, hares attacked a greater proportion of small- than large-diameter stems (see Figure 2).

Impact of Bark and Vascular Tissue Removal on Growth and Survival

The size distribution of girdled and semi-girdled trees in control and spaced stands is illustrated in Figure 3. As expected, trees > 60 mm diameter were not seriously damaged by hares in spaced or control stands. The total percentage of girdled and semi-girdled stems was 30.1% in the control and 18.1% in the spaced stand. An assessment of cumulative damage throughout the study indicated that only 12.9% of control and 6.7% of spaced crop trees were not attacked by snowshoe hares. The number of unattacked trees is reduced further, if squirrel damage is included, with only 8.1% of control and 1.9% of spaced crop trees not damaged by either mammal. Regression analysis indicated that girdling and semi-girdling were significantly related to stem diameters (Figures 3 and 4A).

Analysis of the effect of semi-girdling (50-99% circumference) on diameter increment over the first three growing seasons since spacing was restricted to those diameter classes that had sufficient trees with damage and trees with little (≤ 10 cm^2) or no damage (Figure 4B). In the spaced stand, trees in the 31-50 mm size class with little or no damage grew significantly faster (13.6 mm) than those with semi-girdling (10.9 mm). Similarly, in the control stand, the essentially undamaged trees in the 41-60 mm class grew significantly faster (14.8 mm) than those with semi-girdling (10.0 mm). Damaged control stems ≤ 40 mm diameter had a mean increment of only 6.0 mm (n=9), but an absence of undamaged stems in this size class prevented any comparison. A comparison of undamaged (15.9 mm) and semi-girdled (13.8 mm) stems in the > 60 mm size classes, pooled together for the control stand, was not statistically significant.

TABLE 2. Percentage of trees damaged by snowshoe hares during the winter of 1979-80 in a mixed fir-pine stand.*

	Hare Damage					
	Heavy	Medium	Low	Nil	Girdled	Total (stems/ha)
Species						
Douglas-fir	3(36)	6(73)	8(90)	69(800)	14(164)	1163
Lodgepole pine	25(36)	12(18)	12(18)	12(18)	38(55)	145

*This stand was manually spaced (1308 stems/ha) in the fall of 1978. Sample size in parentheses.

Three-year diameter increments for tree size classes in control and spaced stands are illustrated in Figure 4C. Spaced trees grew significantly faster than did control trees, in terms of diameter, in the 31-70 mm classes. This represents the majority of trees in both stands, and hence is a general conclusion. Although not statistically significant, thinned trees grew better than those in the control in the 71-90 mm classes as well. For the total stand, spaced trees significantly increased their diameter 15.2 mm compared with the control at 13.6 mm. This result is similar to those of Johnstone

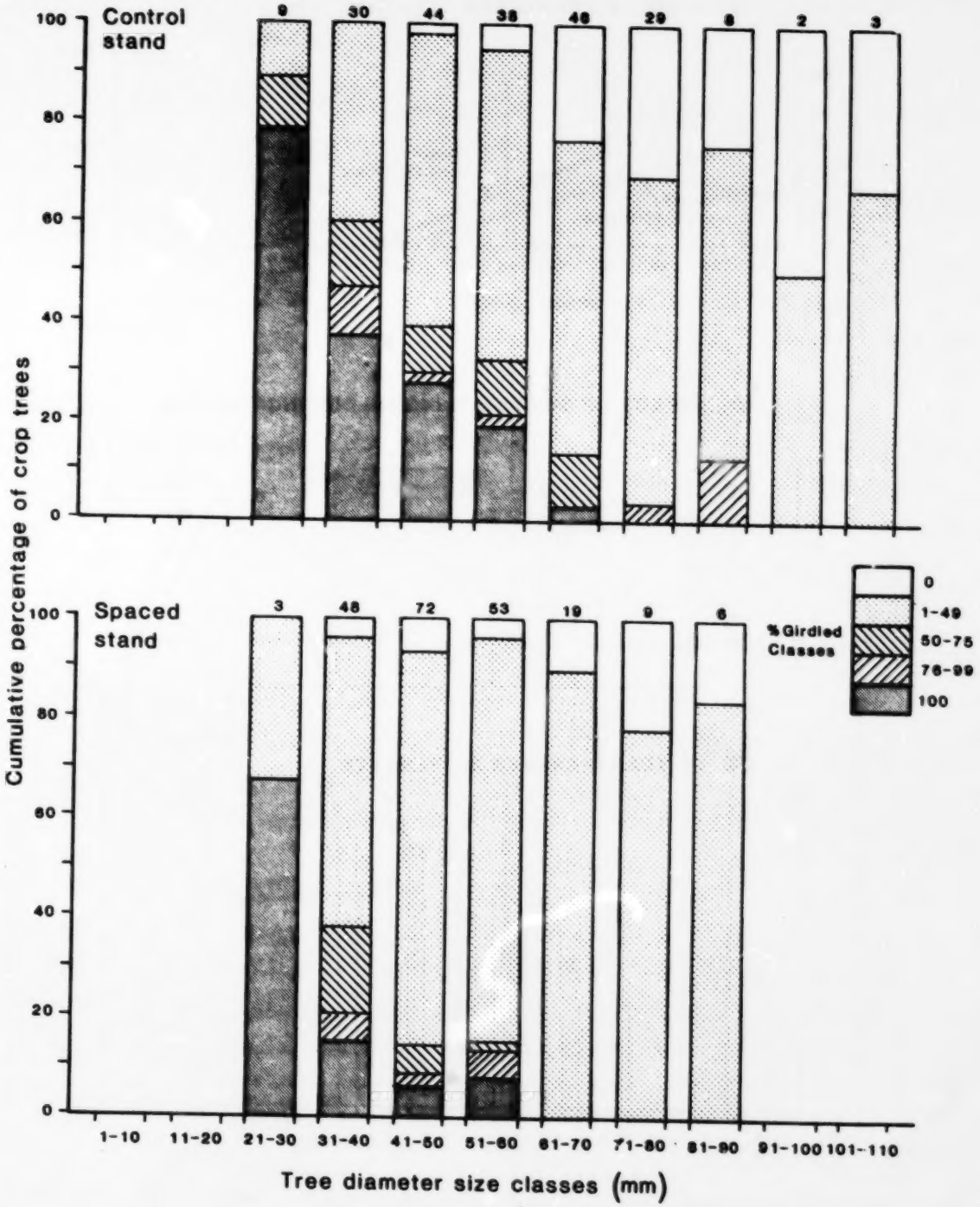


FIGURE 3. Percentage of girdled, semi-girdled, and undamaged crop trees in control and spaced stands of lodgepole pine, 1979-83. Sample size above each bar.

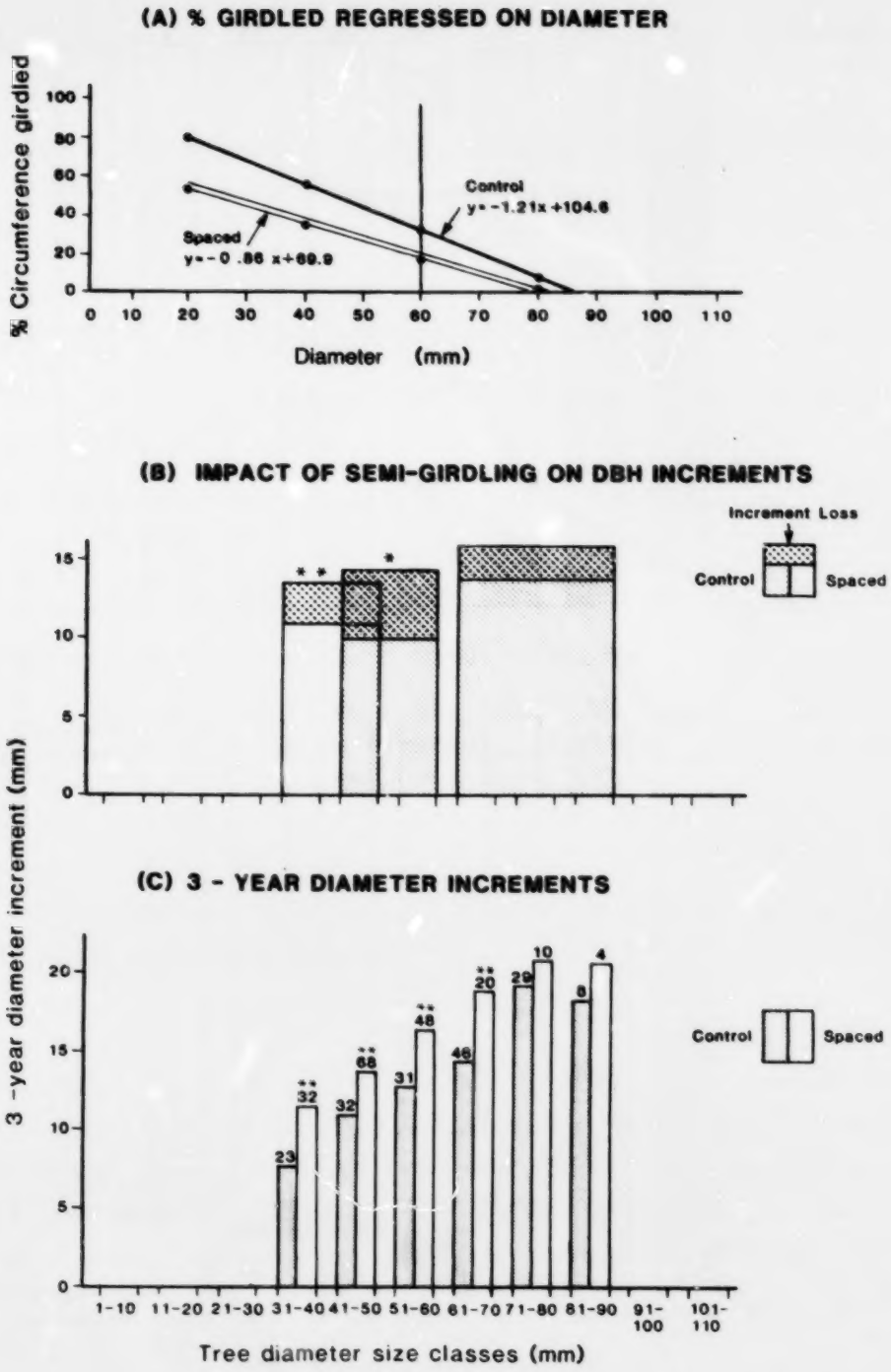


FIGURE 4. Relationship between percent circumference girdled and stem diameter, impact of semi-girdling on loss of diameter increment, and 3-year diameter increments in control and spaced stands.

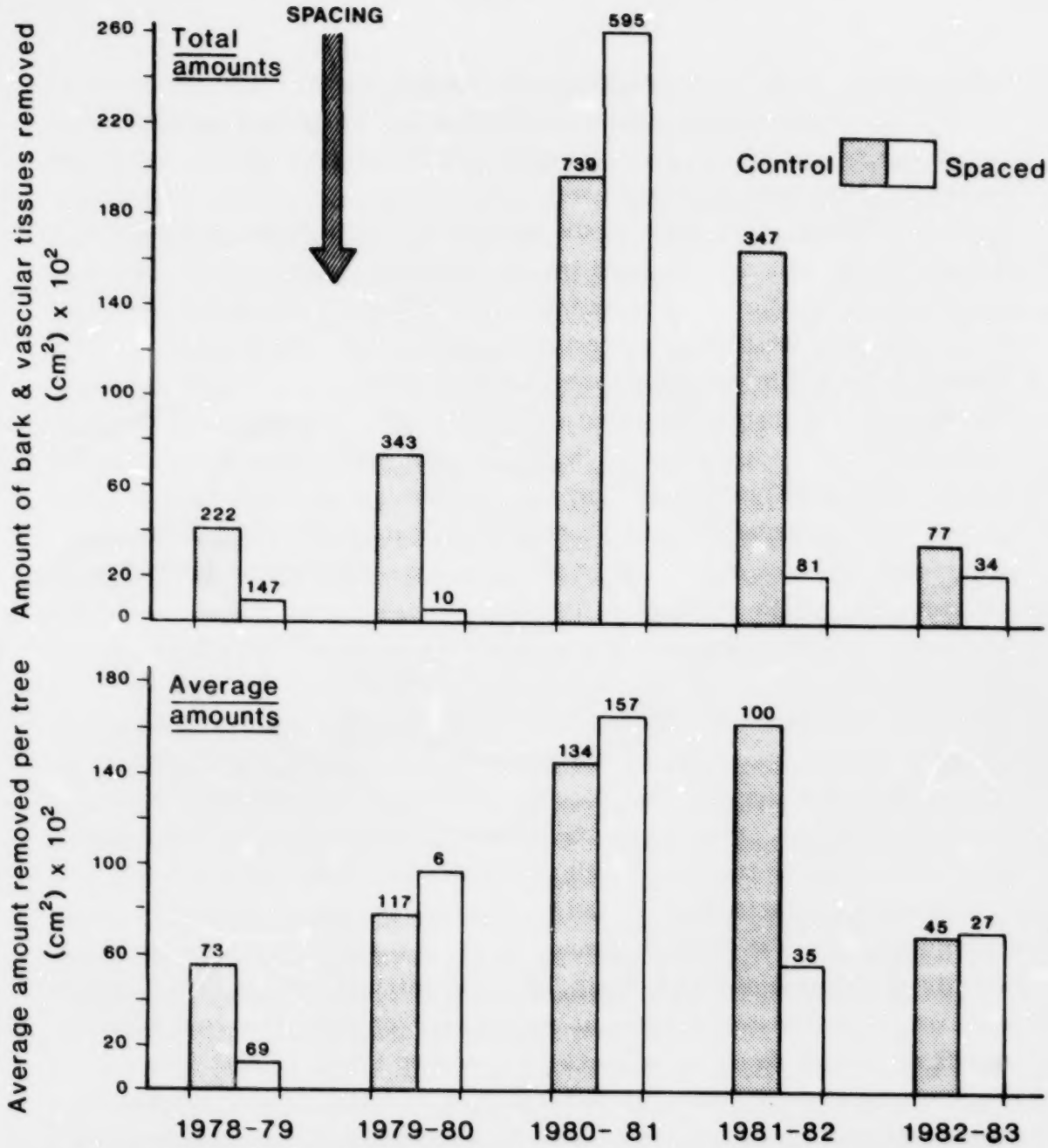


FIGURE 5. Total amount and average amount per tree of bark and vascular tissues removed by hares during five overwinter periods, in control and spaced stands.
Sample size (number of wounds and number of trees) above each bar.

(1981a, 1981b, 1982), and is particularly important because hare semi-girdling (sub-lethal) damage clearly suppressed diameter growth. A similar result for hare damage to balsam fir (Abies balsamea (L.) Mill.) was also recorded in New Brunswick (Lloyd-Smith and Piene 1981).

The surface area of damage is the amount (cm^2) of bark and vascular tissues removed from a given wound through gnawing by hares, and may be considered as a measure of feeding intensity. The total and average amounts of bark and vascular tissues removed from sample crop trees is shown in Figure 5. Feeding intensity by hares increased dramatically in the control from 1979 to 1981, before declining slightly in 1982. In the spaced stand there was little feeding pressure in 1979 nor the year after spacing in 1980. However, over 26 000 cm^2 (2.6 m^2) of bark and tissues were removed from the 157 damaged sample crop trees during the winter of 1980-81. This represents an average of 166.1 cm^2/tree. The amount of feeding declined to just over 2000 cm^2 in 1982.

Analysis of the effect on diameter increment of amount of bark removed over the three growing seasons since spacing (hare and squirrel damage > 100 cm^2) used the 41-60 mm size class for spaced trees, and > 60 mm size class for control trees. In the spaced stand, there was no significant difference between damaged tree increment (15.4 mm) and undamaged tree increment (14.2 mm). However, in the control, damaged trees (18.9 mm) grew significantly faster than those with no, or minimal, bark loss (15.9 mm).

The inverse relationship between surface area of damage and growth strongly suggests that width or circumference of injury is the more important variable in reducing diameter growth, at least initially in the life of the crop tree. The somewhat paradoxical rapid growth of trees that have large amounts of feeding damage (compared with undamaged trees) is most likely a result of the snowshoe hare preference to feed on faster growing (presumably more nutritious) pine. This conclusion is supported by the observation that fertilization significantly increased hare damage to lodgepole pine (Sullivan and Sullivan 1982b).

This apparent lack of an adverse effect due to bark and tissue loss must be treated very cautiously for two reasons. An impact on growth may not become obvious for several years, either because additional wounds may reach a threshold level resulting in physiological stress, or wounds may act as entrance courts for disease or parasites. Hare damage does occur during the winter and into early spring when fungal and related parasites may not be prevalent. However, the economic significance of decay in the wounds incurred from logging and fire has been reported by several authors (Molnar and McMinn 1960; Aho 1977; Etheridge 1978; Filip and Aho 1978). Fungal infection of animal barking wounds may seriously affect lodgepole pine growth and future lumber quality, particularly when they occur so early in the life of a tree. Rundel (1973) has shown the existence of a strong correlation between area of basal fire scars and occurrence of snag tops in mature trees of Giant Sequoia. Similarly, Nordin (1958) for lodgepole pine, and Whitney and Brace (1979) for eastern white pine (P. strobus L.), have outlined the importance of fungi entering damage wounds and their adverse effect on lumber quality.

Distribution of Damage

There was a highly significant difference in tree diameter among plots in both stands. Since semi-girdling injuries had a negative effect on diameter growth rate and generally varied with tree diameter, these injuries were analyzed for their distribution throughout the two stands. The difference in damage among plots was significant and tended towards a clumped distribution (1.64) in the control stand, and a random distribution (1.05) in the spaced stand. In general, those plots with an average tree diameter > 60 mm had lower amounts of girdling-type injuries than plots with trees < 60 mm diameter. There was not a significant difference in average amount (cm^2) of bark and tissue removed by hares per plot for either control or spaced stands.

The clumped distribution of girdling injuries in the control stand is an additional problem to be considered, along with the outright mortality from

complete girdling and the significant reduction in diameter growth from semi-girdling. Clumping of damage, with openings in the stand where trees have died, and slower growth where sub-lethal girdling has been inflicted, will result in uneven stand production. The snowshoe hare has been considered a useful agent for thinning forest stands (Cox 1938). A recent study on hare damage to balsam fir also reached this conclusion (Lloyd-Smith and Fiene 1981). However, aggregation of serious girdling injuries in the control stand in this study makes any suggestion of leaving the thinning to hares as sheer folly.

Snowshoe Hare Populations

The population densities (minimum number alive) of snowshoe hares on the Bowes Creek control and spaced study areas are shown in Figure 6. The two populations exhibited a similar trend in abundance up to August 1979 when the sampling plots were spaced. At that time, the number of hares in the spaced stand did not increase as much as on the control. This was possibly due to the felled pine stems and foliage acting as an alternative food source, thereby lowering trappability. Density increased on the control at the end of August, prior to spacing during September 1979. After thinning, the abundance of hares on the spaced area increased, while the control population declined. During the November 1979 and January and March 1980 sampling periods, there were 1.2 to 1.5 times as many animals in the spaced stand than in the control. This difference was presumably made up by new hares which immigrated to the spaced area for the increased food and cover provided by the fallen pine stems and foliage. During the three sampling periods after spacing, there were 114 new hares captured on the thinned grid and 49 new animals caught on the control.

In the spring of 1980, the number of hares in the spaced stand declined to a level comparable with that of the control. Both populations then increased throughout the summer of 1980, and peaked before declining slightly in the

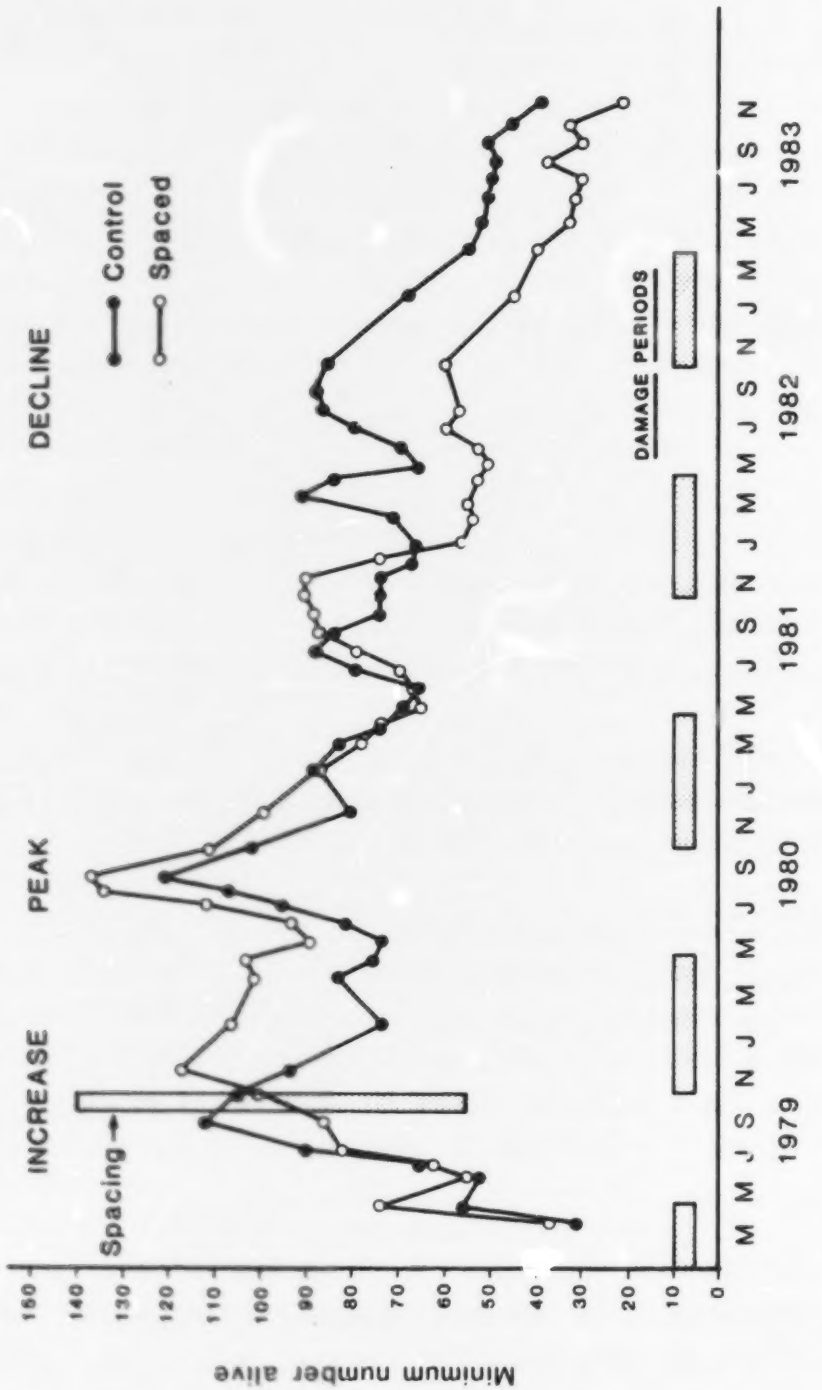


FIGURE 6. Population densities (MNA) of snowshoe hares in control and spaced stands.

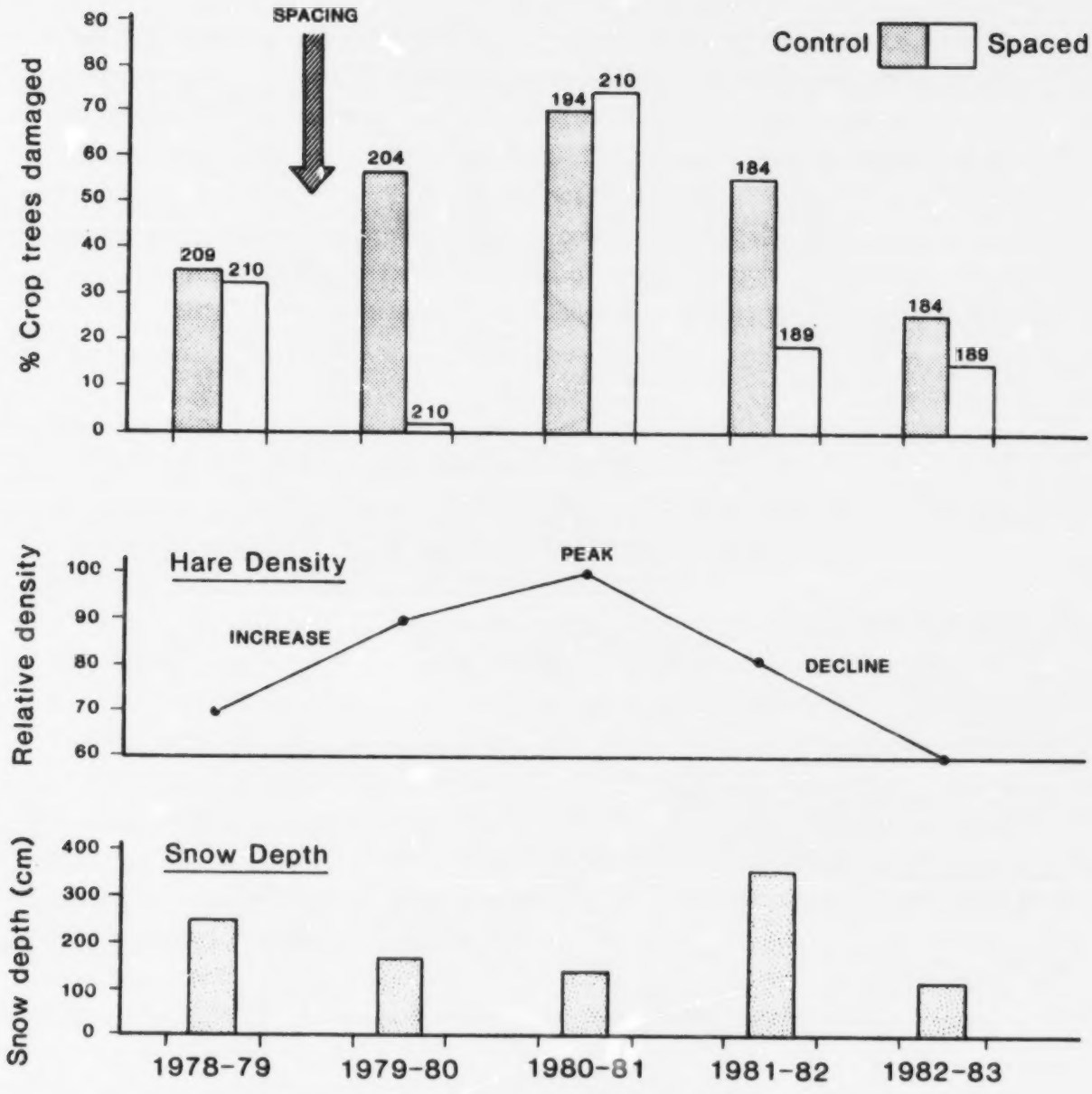


FIGURE 7. Relationship of new snowshoe hare damage intensity, phase of population cycle, and snow depth, for control and spaced stands during 1979-83.

fall-winter of 1980-81. This similarity in density continued throughout most of 1981 until the fall, when the population on the spaced area continued to increase while the control population declined. Both populations declined during the winter of 1981-82. Very few hares occupied the spaced stand because of the heavy snow cover througout the winter of 1981-82 and the population continued a gradual decline during 1982 and 1983. The population in the control stand increased in the spring and fall of 1982, before declining in a similar manner to that in the spaced stand. In general, snowshoe hares were about one-third as abundant in 1983 compared with the peak year of 1980.

Snow Depth

The relationship between damage intensity, phase of population cycle, and snow depth is illustrated in Figure 7. Average snow depth from 1978-79 to 1981-82 was 225.4 $\pm$ 48.6 cm. The four years in which high populations (and feeding damage) occur, during each cyclic peak, indicate increasing variation in snow depth over time: 1950- 257.5 $\pm$ 17.7 cm; 1960- 221.1 $\pm$ 21.8 cm; and 1970- 236.5 $\pm$ 34.5 cm. Since the availability of overwinter food (deciduous and coniferous browse and bark) and cover for snowshoe hares are limited by snow depth, this latter variable may strongly influence the amount of damage sustained by spaced trees in a given winter. Relatively low snow depths ($<$ 150 cm) allow hares to persist in spaced stands and cause considerable damage throughout the winter (e.g., 1979-80, 1980-81). Large amounts of snow (e.g., $>$ 300 cm in 1981-82) resulted in few hares occupying the very open spaced stand. The highly variable total snow depth at Prince George strongly indicates that snow cover cannot be relied upon to minimize damage during peak populations of hares.

CONCLUSIONS

This study has measured the impact of snowshoe hare feeding injuries on thinned lodgepole pine during the first four years after spacing. This period

corresponded with the late increase, peak, and decline phases of the 10-year population cycle. Semi-girdling (sub-lethal) damage clearly suppressed diameter growth of crop trees in both control and spaced stands. Frequency of attack and girdling damage were significantly dependent on tree diameter. The proportion of girdled and semi-girdled trees declined to nil as diameter size classes increased to > 60 mm in the spaced stand. Less than 20% damage is expected in the 60-80 mm classes and no damage in the > 80 mm classes. Therefore, when hare populations begin increasing again in 1987-88 prior to peak numbers in 1990, those spaced trees that have reached a diameter > 60 mm will not be susceptible to damage. Also, the spaced stand will not be as attractive for snowshoe hares because of the larger trees and general lack of food and cover. This trend was apparent during 1982 and 1983 when 20% fewer hares occupied the spaced stand compared with the control stand.

This relationship was also evident from an analysis of hare densities and damage at various stocking levels of lodgepole pine (Sullivan and Sullivan 1983). Because of the inverse relationship between stand density and stand diameter (Sullivan and Sullivan 1982a), it is not surprising that fewer hares and injuries were evident in the stands with 15 000 stems/ha or less. Less dense stands (average dbh=70 mm) could presumably undergo juvenile spacing with little, if any, compensation for future crop tree loss to hares. This index of stocking level susceptibility is applicable to hares only, and is not relevant to squirrels or their damage pattern.

Continued low-intensity monitoring of snowshoe hare populations through the 10-year cycle will verify the above predictions so that recommendations for strategic timing of spacing operations (with low hare populations) will be completely sound. In addition, assessment of damage to crop trees and its impact on growth and yield should be continued -- at least until damaged trees succumb, or survive and grow at rates comparable to undamaged trees.

RECOMMENDATIONS TO ALLEVIATE DAMAGE

1) Juvenile spacing of overstocked stands of lodgepole pine that are susceptible (> 15 000 stems/ha) to hare damage should be delayed until the potential crop trees are ≥ 60 mm average diameter. Overstocked stands < 15 000 stems/ha may be spaced without concern for potential hare damage.

2) Stands with potential crop trees of average diameter ≤ 60 mm may be spaced during the peak year or first year of the decline in the hare population cycle. One year with minimal damage will follow because the fallen pine foliage acts as an alternative food source. However, crop trees must be of sufficient initial size to reach > 60 mm diameter during the six to seven years before the next hare population increase (e.g., 1988).

3) In stands with a wide range of size classes, choose large (> 60 mm) diameter crop trees and, if necessary, leave smaller diameter stems as sacrifice food for hares.

4) A two-step spacing program is the most flexible approach. This strategy would space stands in two stages, dependent on stand age and site factors. Small-mammal damage to closely spaced stands after the initial treatment could be assessed, and the level of treatment in the second stage could compensate for tree mortality without serious crop tree loss. This second-stage thinning assumes that stems have grown beyond susceptibility to hare damage before the stand is treated, and that other potential mortality factors such as disease or insect attack do not appreciably lower the final crop tree density.

5) In terms of area, spacing operations should cover as large an area as possible to render the habitat (spaced stand) less attractive to hare populations over time.

6) A timed-release biological repellent system or a systemic repellent to reduce hare damage during all phases of the population cycle should be developed.

These recommendations cannot be applied to coniferous plantations which, in most cases, must outgrow and survive two and probably three peaks of snowshoe hare populations in central and northern regions of B.C. After this time, trees will presumably have reached a stage where they could be spaced on the basis of crop tree selection.

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